Tiger beetle assemblages in a climatically transitional area of northwestern Costa Rica

(Coleoptera: Cicindelidae)

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Abstract

Along a transect from the Pacific semihumid to the Atlantic perhumid climate in northwestern Costa Rica (eastern Guanacaste National Park), the tiger beetle fauna consists of eight species which, according to their ecological distribution, can be grouped into four species assemblages. These correspond to four major habitat types:
1) abandoned pastures (with one species: *Megacephala fuliginosa* BATES, 1874),
2) tropical moist forests alternating with riparian premontane wet forests (four species: *Ctenostoma maculicorne* CHEVROLAT, 1856, *Oxycheila polita* BATES, 1872, *Odontocheila nicaraguensis* BATES, 1874, *Cicindelidia cyaniventris* (CHEVROLAT, 1834)),
3) premontane rain forests (four species: *Oxycheila polita* BATES, 1872, *Pseudoxycheila tarsalis* BATES, 1869, *Iresia pulchra* BATES, 1881, *Odontocheila iodopleura* BATES, 1872), and
4) lower montane rain forests (one species: *Pseudoxycheila tarsalis* BATES, 1869).
Within each assemblage the species differed well in their different ecological parameters. As a rule, absolute abundances were higher in slightly disturbed habitats (trails) compared to primary habitats (completely undisturbed forest). These results may question the suitability of terrestrial tiger beetles as indicator taxa for the biodiversity of totally undisturbed tropical primary forests to some degree since low densities do not allow a ready and efficient inventory.

Introduction

From the biological point of view Costa Rica is probably the best known Neotropical country. Surprisingly, only little information is available on tiger beetles. This is rather unexpected, because due to their conspicuous diurnal behavior most of the species are easy to observe. Furthermore, tiger beetles are presumed to be good indicator taxa for the biodiversity and habitat quality of tropical environments (e.g., PEARSON 1992, 1994, PEARSON & CASSOLA 1992, RODRIGUEZ et al. 1998).

In contrast to the recent studies of PEARSON and collaborators on South American cicindelid assemblages (e.g., PEARSON 1985, 1992, RODRIGUEZ et al. 1998), studies on Central American assemblages are almost non-existant. For the whole of Central America only PEARSON (1980) gives some information on assemblages of forest dwelling species in Costa Rica and Panama.

The present study was conducted in the eastern part of the Guanacaste National Park, the so called Maritza sector, with the aim to receive autecological data on cicindelids as well as basic information on ecological distribution patterns and species assemblages.

Material and Methods

Study area

The Maritza sector is situated within the eastern part of the Guanacaste National Park (Guanacaste province, north-western Costa Rica) at approximately 11°57'N and 85°29'W. The study area covers the western foothills of Volcán Orosi and Cerro Cacao (at 500 to 700 m a.s.l.), the steep northwestern slopes,
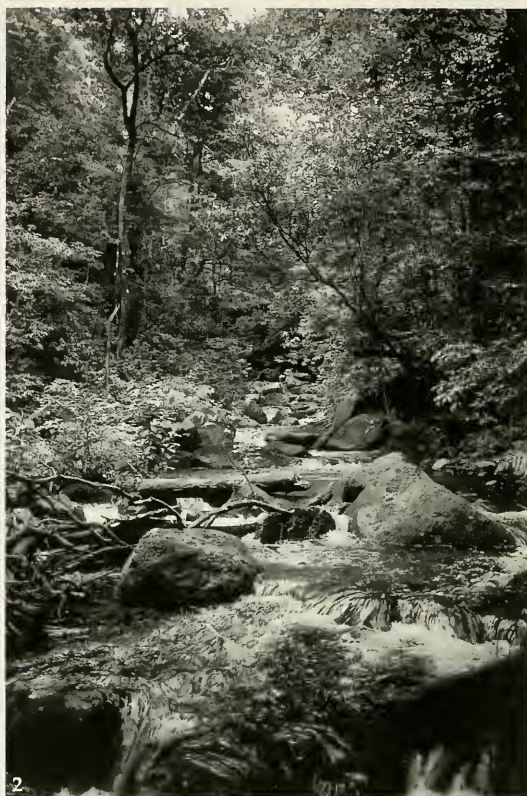
Fig. 1. Trail through secondary growth (formerly Tropical Moist Forest – TMF) south of Maritza Biological Station, 600 m a.s.l. Habitat of *Ctenostoma maculicorne* and *Odontocheila nicaraguensis*.
Fig. 2. Riparian Premontane Wet Forest (RPWF) at 700 m a.s.l. at the base of Cerro Cacao. Individuals of *Oxycheila polita* were found foraging on the large rocks within the riverbed in the foreground.

and the summit of Cerro Cacao (up to 1550 m a.s.l.). Though almost completely located on the Pacific side of the continental watershed (with the exception of the summit of Cerro Cacao), the climate is transitional between Pacific semihumid ("dry forest climate" with a well defined dry season) and Atlantic perhumid ("rainforest climate" without dry season). Within the study site, absolute annual rainfall roughly increases from west to east (along with an increase of elevation), as well as the tendency to a well defined dry season decreases in the same way. However, exact precipitation data for the different life zones are not available. At the present, five major habitat types are to be found within the area (compare TOSI 1969, HARTSHORN 1983), the distributions of which depend on quantity and distribution of precipitation, edaphic situation, elevation and quality of vegetation (disturbed or undisturbed):

– **Abandoned pasture (AP)**. The lower parts of the study site (400-700 m a.s.l.) are partly dominated by open or semi-open, savanna-like stands of mainly Jaragua grass (*Hyparrhenia rufa*), often with sucessions of bushes and small trees and small pockets of secondary growths. The natural vegetation of most of the pasture areas is semi-deciduos tropical moist forest.
– **Tropical Moist Forest (TMF)**. Mainly undisturbed stands of semi-decidous tropical moist forests exist on edaphic dry ridges between small valleys on the foothills of Volcán Orosi and Cerro Cacao (600-700 m a.s.l.). Primary forests are sligthly disturbed by some trails and are often associated with patches of secondary growth (Fig. 1).
– **Riparian Premontane Wet Forest (RPWF)**. An association, similar to the evergreen premontane wet forests of HOLDRIDGE (1967), exists in riparian situations inside of small valleys runnig down from Volcán Orosi and Cerro Cacao (500-700 m a.s.l.: Fig. 2). The presence of this humid forest, with a gallery

Fig. 3. Trail through Premontane Rain Forest (PRF) at 850 m a.s.l. at the northern slope of Cerro Cacao. *Odontocheila iodopleura* was common at this site.

Fig. 4. Trail through Lower Montane Rain Forest (LMRF) near the top of Cerro Cacao at 1500 m a.s.l. Habitat of *Pseudoxycheila tarsalis.*

forest like distribution, is not caused by higher precipitation but by wet edaphic situations and high atmospheric humidity. The forests are undisturbed with the exception of some trails.

– **Premontane Rain Forest (PRF).** The lower and mid elevations (700-1400 m a.s.l.) of the northern slopes of Cerro Cacao are covered by evergreen premontane rain forests (Fig. 3). There is an abrupt change from RPWF to PRF with the first steep slopes in windward situations. With the exception of two clearings and some trails, forests are mostly undisturbed.

– **Lower Montane Rain Forest (LMRF).** Undisturbed evergreen lower montane rain forests (cloud forests, elfin forests: Fig. 4) are present at summit of Cerro Cacao (1400-1550 m a.s.l.). They are undisturbed with the exception of some narrow trails.

Methods

The study was started two months after the beginning of the rainy season in the first days of August and lasted two months until the end of September 1993. During this time, I visited all major habitat types of the area almost daily along a transect, mainly at daytime between 9.00 and 17.00. Night excursions were done only in the environments of the Maritza Biological Station in AP, RPWF and TMF. A total of about 400 man-hours was spent in the field, including rainy days or days with overcasted sky (which are not appropriate for a study on tiger beetles). About 70 % of the time was spent to search on and along trails, while the remainig 30 % were spent outside of this structures (predominantly undisturbed forest). Tiger beetles were detected by walking slowly through potential habitats and looking some meters ahead. As far as not identifiable by observation, beetles were caught by hand or with a net. Because of the efficiency

of this field technique, the additional use of pitfalls was avoided. PEARSON & CASSOLA (1992) state that (using the above mentioned field technique) even unexperienced persons were able to collect 78-93 % of the total species numbers within the first 50 culmulative hours of collecting at three Neotropical rainforest sites (PEARSON & CASSOLA 1992: Tab. 2). Moreover, the cicindelid fauna of the study area consists predominantly of arboreal, semi-terrestrial, and semiaquatic species. Such non-terrestrial species are unlikley to be caught in pitfalls. However, a permanently installed Malaise trap in the understory of undisturbed TMF was regularyly checked for the presence of tiger beetles. The nomenclature used in that of WIESNER (1992).

Results

General aspects

Species' ecological distributions and absolute numbers of observed specimens are shown in Fig. 5 and Tab. 1. During the study seven tiger beetle species were found. Five of them were regulary observed and are regarded as common at the study site, but two (*Ctenostoma maculicorne* CHEVROLAT, 1856, *Cicindelidia cyaniventris* [CHEVROLAT, 1834]) were only taken as single individuals. In the case of *C. maculicorne* this can be easily explained by its arboreal behavior, while the reason for the scarcity of *Cicindelidia cyaniventris* is unclear. This specimen was collected in the first days of the study. Because the habitat where this individual was taken is quite common in the area and the locality was visited almost daily, the species' seasonal activity most probably had already passsed at the time of study. This may also be true for *Megacephala fuliginosa* BATES, 1874, of which only one adult was collected at the beginning of the study. However, larvae were found frequently during the whole study. Another species, which was reported by SUMLIN (1994) from this area (*Iresia pulchra* BATES, 1881), could not be found.

Approximately 280 man-hours of searching along forest pathes yielded more than 180 specimens of terrestrial and semi-terrestrial species (i.e. *Odontocheila nicaraguensis* BATES, 1874, *O. iodopleura* BATES, 1872, *Pseudoxycheila tarsalis* BATES, 1869; Tab. 1). By contrast, only four individuals of *O. nicaraguensis* and five individuals of each of *O. iodopleura* and of *P. tarsalis* were found during approximately 120 man-hours of searching on the undisturbed forest floor (see below).

Species accounts

Ctenostoma maculicorne CHEVROLAT, 1856. A single specimen was found in a young secondary TMF at 600 m a.s.l. in a sunny spot about 0.5 m above the ground on the leaf of an large terrestrial bromeliad (*Bromelia* sp.) (Fig. 1).

Iresia pulchra BATES, 1881. This arboreal species (which could not be found) was recorded for the study area by Sumlin (1994). The locality (Estacion Biologica Cacao, 1000-1400 m) lies within PRF. The microhabitat of the species is unknown.

Megacephala fuliginosa BATES, 1874. At night during light rain on August 5, a single adult specimen was found on a loamy trail in AP, at the border of an abandoned pasture to a patch of dense secondary TMF. Fragments of a second specimen were taken a few days later from a *Latrodectus*-net under a piece of wood in a meadow. Larvae burrows occurred commonly on dirt roads and trails through AP from 500 to 600 m a.s.l. Larvae were frequently observed at night feeding on small crickets.

Tab. 1. Total abundances of regulary observed tiger beetles. **AP**, abandoned pastures; **TMF**, Tropical Moist Forest; **RPWF**, riparian Premontane Wet Forest; **PRF**, Premontane Rain Forest; **LMRF**, Lower Montane Rain Forest.

Habitat type	AP	TMF	RPWF	PRF	LMRF
Megacephala fuliginosa (larval burrows)	>50	–	–	–	–
Odontocheila nicaraguensis	–	>50	>50	1	–
Oxycheila polita	–	–	5	16	–
Odontocheila iodopleura	–	–	1	>50	–
Pseudoxycheila tarsalis	–	–	–	26	1

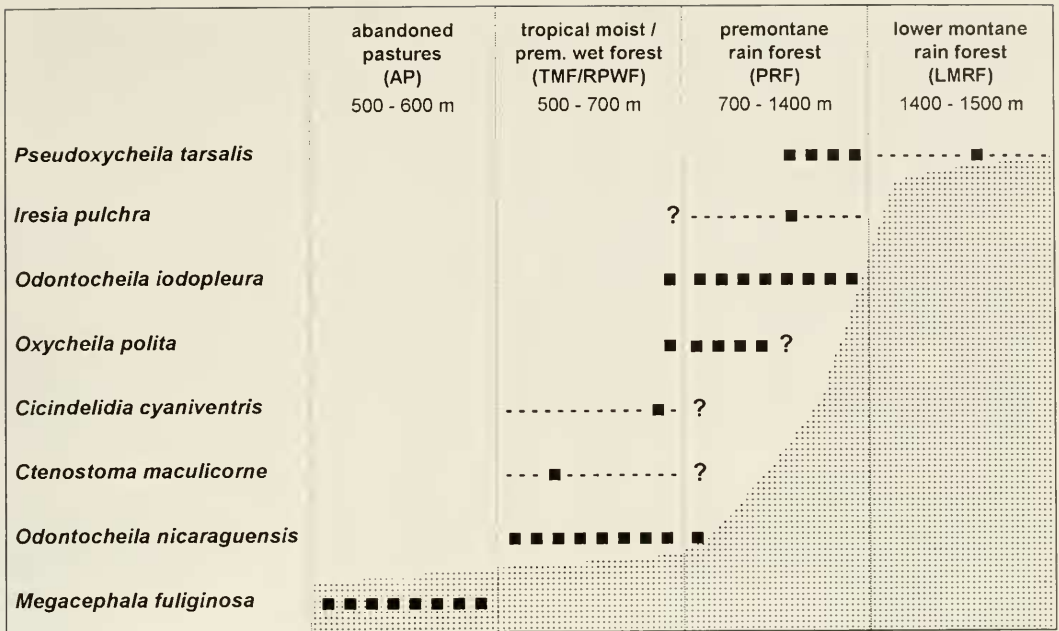|	abandoned pastures (AP) 500 - 600 m	tropical moist / prem. wet forest (TMF/RPWF) 500 - 700 m	premontane rain forest (PRF) 700 - 1400 m	lower montane rain forest (LMRF) 1400 - 1500 m
Pseudoxycheila tarsalis			■ ■ ■ ■ - - - - - - -	■ - - - - -
Iresia pulchra			? - - - - - - - ■ - - - - -	
Odontocheila iodopleura		■ ■ ■ ■ ■ ■ ■ ■ ■	■	
Oxycheila polita		■ ■ ■ ■ ?		
Cicindelidia cyaniventris		- - - - - - - - - - ■ - ?		
Ctenostoma maculicorne		- - - ■ - - - - - - - - ?		
Odontocheila nicaraguensis		■ ■ ■ ■ ■ ■ ■ ■	■	
Megacephala fuliginosa	■ ■ ■ ■ ■ ■ ■			

Fig. 5. Ecological and altitudinal distribution of tiger beetles in eastern Guanacaste National Park, Costa Rica. Locality record of *Iresia pulchra* according to SUMLIN (1994). Shaded background shows the corresponding altitudinal profile of the study area, roughly ranging from Maritza Biological Station in the northwest to the summit of Cerro Cacao in the southeast. Squares indicate the proofed distributions, broken lines potential distributions. Questionmarks indicate uncertain distribution limits.

Oxycheila polita BATES, 1872. The species was regulary observed in two small, 5-10 meters wide, rapid flowing rivers within RPWF and PRF between 600 and 800 m a.s.l (Fig. 2). Individuals were found foraging on large rocks (with a thin moss and algae cover) and logs within the riverbed and on broad-leafed plants bordering its banks. When disturbed, beetles frequently entered the water on the downstream side of rocks or logs (water temperature around 22 °C). Highest density was 5 specimens/100 m river. Copulation was observed several times during the whole study time. At one occasion, the semiaquatic lizard *Norops oxylophus*, which is a typical inhabitant of riparian habitats at Maritza, was observed hunting *O. polita*.

Pseudoxycheila tarsalis BATES, 1869. This species was commonly found within PRF on a loamy, broad forest trail on Cerro Cacao between 1100 and 1200 m a.s.l. Maximum density was 8 specimens/100 m trail. The lowermost sighting at the study site was at 900 m a.s.l., where five individuals were observed on bare ground at a tree fall in dense undisturbed primary forest on a steep loamy slope. Additional single specimens were taken near a building on a loamy path across a large, grassy clearing at 1100 m (Estacion Biologica Cacao) and on a narrow trail across an small open area in lower montane rain forest at 1500 m near the summit of Cerro Cacao (Fig. 4). All localities had only a sparse cover of leaf litter with small patches of bare ground. When disturbed, most individuals tried to escape by running into leaf litter, small twigs or low vegetation. Most of the specimen observed were active in small sunny spots, while shaded areas or a search during overcasted sky yielded only a few animals. Copulation was observed in one instant on August 27, 1993.

Odontocheila nicaraguensis BATES, 1874. *O. nicaraguensis* was common on trails through primary and secondary TMF and RPWF at 500-700 m a.s.l. The species was regulary found in shade or semi-shade but seemed to prefer sunny spots. The most frequently observed habitat, which yielded maximum densities of up to 15 specimens/100 m trail, were forest trails with some herbaceous vegetation, spots of bare ground, and sparse leaf litter (Fig. 1). Beside that, single specimens were found in undisturbed, dense forest. One of these specimen was the only tiger beetle captured in the Malaise trap (dense understory of primary TMF). Three other individuals were observed one on bare ground at a treefall, the other on a steep

embankment near a small river, and the third at a nest of leaf-cutting ants. As a rule, *O. nicaraguensis* was most common in such places, which had a constant supply of ground humidity. It did not occur on well drained and comparatively dry forested ridges and in the stony floodplains of small rivers. Densities were highest during sunny weather, but even during light rain a few animals were frequently observed. The species was found foraging on the ground as well as in low herbaceous vegetation, but when disturbed all animals flew into low vegetation. The escape distance was about 2 m and the escape flights ranged from 1 to 5 m. The perch heights after landing was between 0.3 and 1.5 m above the ground. Copulations were observed frequently throughout the study period.

Odontocheila iodopleura BATES, 1872. On the steep north-western slopes of Cerro Cacao in PRF at 700-1300 m, *O. iodopleura* ecologically replaces *O. nicaraguensis*. It was common along narrow trails through primary forests (Fig. 3). The prefered microhabitats of *O. iodopleura* are identically with those of *O. nicaraguensis* (see above), with the exception that the first species apparently avoids the centers of larger sunny areas (e.g. small clearings) and was more often observerd among totally shaded situations. On a steep loamy slope five additional individuals were observed on bare ground at a fallen tree within dense undisturbed forest. Maximum densities was 20 specimens/100 m trail. Copulation was observed several times only on August 26. The escape distance was as low as 0.5-1 m and the short escape flights ranged from 0.3 to 1.5 m.

Cicindelidia cyaniventris (CHEVROLAT, 1834). A single specimen was collected on August 6 on a trail through a 5-10 m tall secondary growth of presumedly TMF at 650 m a.s.l. The locality was totally shaded and offered small spots of humid, bare, loamy soil among large areas covered by leaf litter. This specimen made no attempt to escape by flight.

Ecological distribution and species assemblages

The distributional data suggest the presence of four distinct tiger beetle species assemblages in the five major habitats along the transect (Fig. 5, Tab. 1). These are associated with (1) abandoned pastures, (2) Tropical Moist Forests/Riparian Premontane Wet Forests, (3) Premontane Rain Forest, and (4) Lower Montane Rain Forest.

Each of the four major habitats had a unique species assemblage. Within AP and LMRF only a single adult specimen of each species each was found (*Megacephala fuliginosa* and *Pseudoxycheila tarsalis* respectively). Although recorded only once in LMRF, *P. tarsalis* is presumed to have a wider distribution here. There are suitable habitats to some extant and this life zone is well inside the species' ecological distribution in Costa Rica (PALMER 1976, 1983). The meager results of my research were certainly caused by the constantly overcasted to rainy weather during all visits in the cloud forest.

TMF/RPWF and PRF are each inhabited by assemblages of four sympatric species (Tab. 2). I combined

Tab. 2. Parameters of niche segregation in forest tiger beetles assemblages of two major habitats in the eastern part of the Guanacaste National Park, Costa Rica. Total length (without labrum) rounded to nearest half mm; body size of *Iresia pulchra* according to SUMLIN (1994).

Species	Total length [mm]	Habitat	Prefered insolation
Tropical moist/Riparian Premontane Wet Forest (TMF/RPWF)			
Ctenostoma maculicorne	12.0	arboreal	?
Odontocheila nicaraguensis	12.5-15.0	semi-terrestrial	sunny/shaded
Cicindelidia cyaniventris	11.5	terrestrial	?
Oxycheila polita	15.5-17.0	semiaquatic	sunny/shaded
Premontane Rain Forest (PRF)			
Iresia pulchra	8.0-10.0	arboreal	?
Odontocheila iodopleura	8.5-11.0	semi-terrestrial	shaded
Pseudoxycheila tarsalis	15.0-17.0	terrestrial	sunny
Oxycheila polita	15.5-17.0	semiaquatic	sunny/shaded

TMF and RPWF on the basis of the common occurrence of *Odontocheila nicaraguensis* in both zones and its nearly complete absence in other zones (see below). However, the species was most common at more humid sites (e.g. riparian forest or edaphic humid places) and did not occur on the dryest ridges of TMF. Furthermore *Ctenostoma maculicorne* and *Cicindelidia cyaniventris* are presumed to have a wider distribution both in TMF and RPWF.

The distribution of two species overlapped slightly at the transition of TMF/RPWF and PRF: in one case, a specimen of *O. iodopleura* was taken inside a secondary RPWF near to PRF among several *O. nicaraguensis*. Vice versa, a single individual of *O. nicaraguensis* was observed among several *O. iodopleura* in PRF near to RPWF.

In the major habitats where more than one species occurred, sympatric tiger beetles differed well in their ecological parameters (Tab. 2): TMF/RPWF is inhabited by *Odontocheila nicaraguensis* and *Oxycheila polita*, which are both comparably common. Two other species were found only as single individuals (*Ctenostoma maculicorne, Cicindelidia cyaniventris*). The habitat use of these four species is obvious: one arboreal (*C. maculicorne*), one semiaquatic (*O. polita*), and two forest floor species; the latter being different in body size and presumably also in microhabitat use and activity seasons: *C. cyaniventris* being the smaller, exclusively terrestrial species with a probable adult activity only during the beginning of the rainy season.

PRF is inhabited by *Pseudoxycheila tarsalis, Oxycheila polita, Iresia pulchra*, and *Odontocheila iodopleura*. Under consideration of a wide occurrence of *I. pulchra* within PRF, the species assemblage again consists of one arboreal (*I. pulchra*), one semiaquatic (*O. polita*), and two terrestrial species; the latter two differing in bodysizes and microhabitats: *P. tarsalis* being a large, exclusively terrestrial species preferring sunny places; *O. iodopleura* being a small species, inhabiting low vegetation and prefering more shaded situations.

Discussion

General aspects, ecological distribution, and species assemblages

Available information on habitat preferences of some of the species agree well with literature data (e.g., *Ctenostoma maculicorne*: NAVIAUX 1998 for the genus; *Oxycheila polita*: CUMMINS 1992; *Pseuoxycheila tarsalis*: PALMER 1976, 1983, CASSOLA 1997; *Cicindelidia cyaniventris*: MURRAY 1979 for Mexican populations).

The present study reflects only a temporarily limited aspect of the tiger beetle assemblage of the Maritza area, namely the mid rainy season. Though mid rainy season is presumed to be a good time for an inventory of tiger beetles in the tropics (PEARSON & DERR 1986), the observations of just one adult individual of *Megacephala fuliginosa* and *Cicindelidia cyaniventris* each at the beginning of the study time suggests that the activity period of these two species had already passed. It is known that species composition of assemblages and habitats of tiger beetles change markedly with the dry and the rainy season in the tropics (PEARSON & DERR 1986, PEARSON 1988). FAHR (unpublished manuscript) found that in a climatically semihumid area in West Africa relative abundance and habitat use of cicindelids changed considerably even during the rainy season.

One of the most remarkable facts of the present study is the complete lack of diurnal, non forest-dwelling species in the study area. Such species are common members of tiger beetle assemblages in other parts of the Neotropics (e.g., PEARSON et al. 1993, PEARSON & HUBER 1995, RODRIGUEZ et al. 1998) as well as in the Old World tropics. The explanation may be easy: although heavily deforested at present (with many savanna-like areas in the Guanacaste National Park) the whole nonswamp area of northwestern Costa Rica is presumed to have been completely forested in the past (HARTSHORN 1983, JANZEN 1986). Consequently, species restricted to open, terrestrial habitats are unlikely to occur in the study area. Throughout the tropics the occurrence of diurnal terrestrial (non-riparian) tiger beetles of open habitats seems to be linked to the occurrence of naturally open habitats like grasslands or thorn forests.

PEARSON (1980) found *Odontocheila nicaraguensis* and *O. iodopleura* occurring together in a Caribbean lowland rainforest in Costa Rica, as well as an equivalent species pair of similar divergent sizes throughout several lowland rainforest sites in Costa Rica, Panama, Ecuador and Bolivia. By contrast, *O. nicaraguensis* and *O. iodopleura* are well differentiated at Maritza with respect to their ecological distribution. The only exception is a small transitional zone at the foot of Cerro Cacao. This situation is perhaps caused by the transitional character of climate at the study area. There is a well defined dry season of 4-5 months at the lower pacific foothills (where *O. nicaraguenis* occurs) which is probably not suitable for *O. iodopleura*. Vice versa those areas at the mid-elevation slopes of Cerro Cacao, which receive sufficient humidity for *O. iodopleura*, are presumedly too cold for *O. nicaraguensis*.

Tiger beetles are known to have several strategies to minimize competition among sympatric species. Most commonly, temporal or spatial separations occur (WILLIS 1967, RUMPP 1977, KNISLEY 1984, GANESHAIAH & BELAVADI 1986, SCHULTZ & HADLEY 1987, SCHULTZ 1989). PEARSON & MURY (1979) and PEARSON (1980) found that among co-occurring species divergent mandible sizes occurs, which force each species to forage on a different part of a prey spectrum. In the case of the Maritza beetles spatial separation seems to minimize competiton within adult species' assemblages during the study time at mid-rainy season. However, temporal separations are likely to occur as well.

Are tiger beetles really appropriate indicator taxa for tropical forests?

Pearson and collaborators suggested the use of tiger beetles as indicator taxa for biodiversity and monitoring studies in tropical environments (PEARSON 1992, PEARSON & CASSOLA 1992, PEARSON & HUBER 1995, RODRIGUEZ et al. 1998). Two of the major arguements for this are (1) that tiger beetles can be readily surveyed, even by inexperienced persons, and (2) that on lower taxonomic level specialization on a narrow habitat makes them sensitive to habitat changes. In a study on Venezuelan species' assemblages RODRIGUEZ et al. (1998) found that primary, semi-disturbed, and disturbed forest each had a characteristic species assemblages, depending on the degree of disturbance. In the present study the habitats are similar to those investigated by RODRIGUEZ et al. (1998). In general, my own results support the findings of the study in Venezuela: the only heavily disturbed major habitat at Maritza (AP) had a completely different faunal structure (only a single nocturnal species) than the other, more or less primary habitats. However, none of the places at Maritza where larger number of terrestrial tiger beetles occurred, are really primary. All microhabitats which yielded more than single specimens – even within large areas of undisturbed primary forest – are associated with man-made trails. Completely natural microhabitats (e.g., bare ground at fallen trees, bare areas at nests of leaf cutting ants) are rather restricted and were inhabited by only a very few individuals. Additionally, in the case of *Odontocheila nicaraguensis*, there were no differences in relative abundance on trails through primary forest compared to trails through secondary growth. It thus seems that the overall high densities of tiger beetles in the whole area is primarily caused by human activities. The situation at the Venezuelan sites of RODRIGUEZ et al. (1998) might not be very different: transects were established along forest trails, too.

These results question the suitability of terrestrial tiger beetles as indicator taxa for the biodiversity and habitat quality of tropical forests to some degree. It is of course very likely that the "trail-fauna" of otherwise undisturbed forests represents the "natural fauna" with respect to their species composition, but abundances seem to be artifical. From a methodical point of view, the presence of only restricted and small populations in a *completely* natural tropical forest (without trails) does not seem to be appropriate for a efficient inventory use. However, further studies should be done on distribution and densities of tiger beetles of completely primary versus slightly disturbed tropical forests.

References

CASSOLA, F. 1997: Studies on tiger beetles. XC. Revision of the Neotropical genus *Pseudoxycheila* GUÉRIN, 1839 (Coleoptera, Cicindelidae). – Fragm. Entomol. **29**, 1-121.

CUMMINS, M. P. 1992: Amphibious behavior of a tropical, adult tiger beetle, *Oyxcheila polita* BATES (Coleoptera: Cicindelidae). – Coleopt. Bull. **46**, 145-151.

FAHR, J. unpublished MS: Die Sandlaufkäfer (Cicindelidae: Coleoptera) des Comoé-Nationalparks, Elfenbeinküste: Faunistik, Zoogeographie und Ökologie. – 35 pp.

GANESHAIAH, K. N. & V. V. BELAVADI 1986: Habitat segregation in four species of adult tiger beetles. – Ecol. Entomol. **11**, 147-157.

HARTSHORN, G. S. 1983: Introduction (to Plants). In: JANZEN, D. H., Costa Rican Natural History. – Chicago, University of Chicago Press, 118-157.

HOLDRIDGE, L. R. 1967: Life Zone Ecology. Revised edition. – San José, Tropical Science Center.

JANZEN, D. H. 1986: Guanacaste National Park: Tropical ecological and cultural restoration. – San José, Editoral Universidad Estatal a Distancia.

KNISLEY, C. B. 1984: Ecological distribution of tiger beetles (Coleoptera: Cicindelidae) in Colfax County, New Mexiko. – Southwest. Nat. 29, 93-104.

MURRAY, R. R. 1979: The *Cicindela* fauna of Mexico: range extensions, additions, and ecological notes (Coleoptera: Cicindelidae). – Coleopt. Bull. 33, 49-56.

NAVIAUX, R. 1998: *Ctenostoma* (Coleoptera, Cicindelidae). Revision du genre et description de noveau taxons. – Soc. Entomol. Fr., Mem. No. 2.

PALMER, M. 1976: Natural history and behavior of *Pseudoxychila tarsalis* BATES. – Cicindela 8, 61-92.

PALMER, M. 1983: *Pseudoxychila tarsalis* (Abejón Tigre, Tiger beetle). – In: JANZEN, D. H., Costa Rican Natural History. – Chicago, University of Chicago Press, 765-766.

PEARSON, D. L. 1980: Patterns of limiting similarty in tropical forest tiger beetles (Coleoptera: Cicindelidae). – Biotropica 12, 195-204.

PEARSON, D. L. 1985: The tiger beetles (Coleopterea: Cicindelidae) of the Tambopata reserved zone, Madre de Dios, Perú. – Rev. Peru. Entomol. 27, 15-24.

PEARSON, D. L. 1988: Biology of tiger beetles. – Annu. Rev. Entomol. 33, 123-147.

PEARSON, D. L. 1992. Tiger beetles as indicators for biodiversity patterns in Amazonia. – Res. Explor. 8, 116-117.

PEARSON, D. L. 1994: Selecting indicator taxa for the quantitative assessment of biodiversity. – Philos. Trans. R. Soc. Lond. B Biol. Sci. 345, 75-79.

PEARSON, D. L. & F. CASSOLA 1992: World-wide species richness patterns ot tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. – Conserv. Biol. 6, 376-391.

PEARSON, D. L. & J. A. DERR 1986: Seasonal patterns of lowland forest floor arthropod abundance in southeasten Perú. – Biotropica 18, 244-256.

PEARSON, D. L. & R. L. HUBER 1995: The tiger beetles of Pakitza, Madre de Dios, Peru: identification, natural history and a comparison to the Peruvian fauna (Coleoptera: Cicindelidae). – Cicindela 27, 1-28.

PEARSON, D. L. & E. J. MURY 1979: Character divergence and convergence among tiger beetles (Coleoptera, Cicindelidae). – Ecology 60, 557-566.

PEARSON, D. L., BRZOSKA, D. W. & J. F. GUERRA 1993: Rediscovery of *Pometon singularis* FLEUTIAUX (Coleoptera: Cicindelidae) and notes on its natural history in southeastern Bolivia. – Cicindela 28, 12-29.

RODRIGUEZ, J. P., PEARSON, D. L. & R. ROBERTO BARRERA 1998. A test for the adequacy of bioindicator taxa: are tiger beetles (Coleoptera: Cicindelidae) appropriate indicators for monitoring the degradation of tropical forests in Venezuela? – Biol. Conserv. 83, 69-76.

RUMPP, N. L. 1977: Tiger beetles of the genus *Cicindela* in the Sulphur Springs Valley, Arizona, with descriptions of three new subspecies (Cicindelidae – Coleoptera). – Proc. Calif. Acad. Sci. 41, 169-181.

SCHULTZ, T. D. 1989: Habitat preference and seasonal abundances of eight sympatric species of tiger beetles (Coleoptera, Cicindelidae) in Bastrop State Park, Texas. – Southwest. Nat. 34, 468-477.

SCHULTZ, T. D. & N. F. HADLEY 1987: Microhabitat segregation and physiological differences in co-occurring tiger beetle species *Cicindela oregona* and *C. tranquebarica*. – Oecologia 73, 363-370.

SUMLIN, W. D., III. 1994: Studies on Neotropical Cicindelidae V: A review of the genus *Iresia* (Coleoptera). – Cicindelidae: Bull. Wldw. Res. 3, 1-32.

TOSI, J. A. 1969: República de Costa Rica. Mapa Ecológico. – San José, Centro Cientifico Tropical.

WIESNER, J. 1992: Verzeichnis der Sandlaufkäfer der Welt – Checklist of the Tiger Beetles of the World. – Keltern, Verlag Erna Bauer.

WILLIS, H. L. 1967: Bionomics and zoogeography of tiger beetles of saline habitats in the Central United States (Coleoptera, Cicindelidae). – Univ. Kans. Sci. Bull. 47, 145-313.

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